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THE RELATIONSHIP OF THE TURTLES AND PLESIOSAURS, . *Roy L. Moodie.*

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THE RELATIONSHIP OF THE TURTLES AND PLESIOSAURS.

BY ROY L. MOODIE.

(Contribution from the Zoölogical Laboratory, No. 182.)

Two text figures.

THE question of the relationship of the turtles and plesiosaurs has interested zoölogists since the time of Buckland, when the nature of the latter animals was first clearly understood. At about this time, too, the first comparisons were made between them. Conybeare compared the plesiosaur to a "turtle stripped of its shell." Mantell remarked that the structure of the plesiosaurs was such as to "justify the graphic simile of an eloquent professor, that the plesiosaurus might be compared to a serpent threaded through the shell of a turtle."[1] Again, Mantell tells us that the "plesiosaurus" combines the characters of several orders of reptiles and has "paddles like the turtle." Ever since the utterance of these statements an affinity between the two groups has been claimed, and this has been based on various grounds. It is the purpose of this essay to review the bases for the relationship and to discover, if possible, the exact conditions in regard to the so-called affinity.

Parker stated that on account of the greater number of segments in the neck and tail of certain turtle embryos that there was a suggestion of relationship between the turtles and plesiosaurs. He strengthened this suggestion by the statement that some of the Cretaceous Chelonia possessed teeth. Seeley called attention to the similarity in the method of ossification of the limb bones in turtles and plesiosaurs, and referred to

1. Mantell, 1851, Petrifactions, London, p. 341.

"conical epiphyses" which penetrate into a cylindrical sheath "so as to meet, or nearly meet, in the center." The turtles and plesiosaurs both have a very peculiar scapula. In both groups it is fundamentally biradiate, and it has been claimed that this condition of the scapula is due to the fusion of the procoracoid to the true scapula in both groups and the homologous mode of formation of this element was made the basis for relationship. Further relationship has been claimed on the fact that the broad character of the pectoral and pelvic girdles of the plesiosaurs resembles to some extent the plastron of the turtles, and there has been some attempt to correlate the elements in the two groups. There is, also, an undoubted similarity in the manner of life of the two groups, and this has been a claim to affinity.

The question of the relationship of the turtles and plesiosaurs has been discussed by various authors, notably Seeley, Hulke, Baur and Williston. An impetus toward the final conclusion of the matter has been given by the recent studies of Williston on the skull of *Brachauchenius,* and by the author's studies on reptilian epiphyses.[2]

The first basis of relationship to be discussed is that of the number of segments in the neck and tail of turtle embryos, first brought forward by Parker.[3] He says (p. 50): "One of the most remarkable things in the embryo (of the green turtle) is the large number of somatomes, in the neck especially, and also in the tail, as compared with what is seen in the intercalary bony segments (vertebræ) of the adult; thus the embryo suggests an ancestry having a longer neck and tail than existing forms. As some of the Cretaceous Chelonia certainly possessed teeth, . . . it is evident that the modern Chelonia are forms that have become separated from their near reptilian relations by specialization. A long-necked ancestry with a fully developed carapace and many bones of the plastron arranged triserially would bring us near the plesiosaurs."

Parker has figured (plate I, fig. 3) an embryo of *Chelone viridis* Schneid., with fifteen somites in the neck and thirty-six in the remainder of the body. The somites as he has figured them in the neck are very unnaturally crowded and packed, and indeed Parker himself noticed this fact. He says that in the development there are seven "somatomes" lost from

2. Moodie, 1908, Amer. Jour. Anat., vol. VII, p. 443.

3. Parker, 1880, Zoölogy Challenger Expedition, vol. I, pt. V.

the neck. The body portions remain as they are, and three are lost from the tail. The manner of development of the tail is not of importance in this connection, so that will not be discussed here. So far as I can learn, Parker's observations as to the large number of somites in the neck have never been confirmed. They certainly are not confirmed by the figures given by Rathke and Agassiz. Nor am I able to find any indication of supernumerary segments in the twoscore or more embryos I have examined, both in sections and whole. I am at a loss to explain Parker's observations, unless it be that his material was pathological. He had only a few specimens at most, and he fails to state how many show this remarkable character. I have carefully examined embryos of several genera of turtles and find nothing unusual in any of them. Before the cartilage is laid down for the vertebræ there are, of course, the somites, but I have never detected any unusual number nor have I seen more than eight cartilages for the vertebræ of the neck. So far, then, as the evidence goes, Parker's results are at variance with the results obtained by others. It can at least be said that the condition described by him for the embryo of *Chelone viridis* Schneid. does not apply to the other turtle embryos examined, and it is to be greatly doubted if there are ever more than the usual number of segments in the normal embryo. So far as I can learn there are no evidences of a reduction, ontogenetically, of the number of segments in the neck of any form, although such has been claimed for some of the birds. It is a matter which is easily conceivable that the loss or addition of vertebræ in the column may take place, and Baur has cited a few such cases. This is, however, by intercalation, and just what its significance is I do not know. Such an instance has never, I believe, been recorded for the turtles, and there is no evidence that the Chelonia ever had more than eight cervicals, while the plesiosaurs had from thirteen to seventy-six.

Teeth have never been discovered in the turtles. Marsh, it is true, described[4] the anterior portion of a peculiar mandible which he suggested might belong to the Chelonia. He says: "So far as now known, they appear to be nearest allied to the Chelonia, although turtles without teeth occur in the same strata with them." Hay says the fossil is problematical, and locates the form, *Macelognathus vagans* Marsh, among the

4. Marsh, 1884, Amer. Jour. Sci., p. 341.

Dinosauria. Teeth buds have been discovered in the embryos of *Trionyx* and *Chelone* by Röse[5], but the presence or absence of teeth in the turtles, unless of a particular type, would be of no classificatory value. Teeth have been aborted for so long in the Chelonia that their form cannot be determined from the embryonic vestiges.

The "conical epiphyses" which have been referred to as present in turtles and plesiosaurs are not epiphyses at all, but are endochondral cones such as are found in all the groups of the Sauropsida, and they are represented by cartilaginous cones in the Amphibia. The term "epiphyses" was first applied to these structures by Seeley,[6] who used the term inadvertently, I believe, and did not at all intend to convey the idea that there were present in the turtles and plesiosaurs "characteristically mammalian elements."[7] That these structures are not epiphyses is well shown by the condition found in

FIG. 1.

the limb bones of certain lizards. In the humerus of the Galapagos lizard, *Amblyrhynchus*, for example, there are present three sets of structures. These are the peri- and endochondral tissues and the terminal bony epiphyses, which differ from the mammalian epiphyses in that they are in part formed of calcified cartilage. Epiphyses are always situated at the ends of bones and never penetrate the shaft to any extent. The so-called epiphyses in turtles and plesiosaurs penetrate the cylindrical shaft and almost meet in the center. These structures persist throughout the life of the individual, of the plesiosaurs at least, but in the turtles they are not so persistent. In some forms of the Chelonia the endochondral cones are replaced by cancellated bone. The manner of development of the cones and perichondral cylinder is well shown in figure 1. The fibers of bone are densest near the middle of the shaft and splay out near the ends of the bone. The endochondral

5. Röse, Carl, 1892, Anat. Anz., Bd. VII, p. 748.

6. Seeley, 1887, Phil. Trans., p. 191.

7. Osborn, 1903, Mem. Am. Mus. Nat. Hist., vol. I, pt. VIII, p. 465.

cone occurs within the perichondrium. Neither turtles nor plesiosaurs have epiphyses, and there is, hence, no basis for relationship between the two groups so far as these structures are concerned.

The relations and shape of the pectoral girdle have also been used as a basis for relationship of the groups under discussion. It has been claimed that the biradiate character of the scapula in the two groups is due to the fusion of the procoracoid with the true scapula. The fact that the fusion was alike in the two groups is, therefore, taken as a basis of relationship. In neither group, however, has this fusion taken place. I have recently studied the development of the skeleton in the Chelonia and hope to present a full discussion elsewhere.

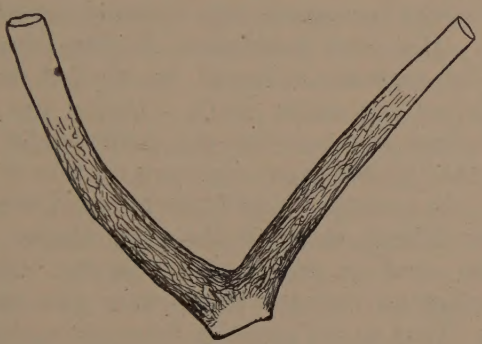

FIG. 2.

The question which interests us here is the condition of the scapula in the early chelonian embryos. In turtles, as has been stated, the scapula is a biradiate element. If it were a composite element there should appear, in the early embryonic stages, at or near the center of the shaft of each prong, a center of ossification, or at least a center of calcification in the very early stages. Specimens have been cleared by the Schultze method, recently set forth by Mall, Hill and myself, and in these specimens it has been possible to ascertain the exact condition of affairs.

The method of ossification in the embryos of reptiles is very peculiar. The bony matter is laid down in long wavy threads, which extend in a cylindrical shaft around the central part of the bone, being densest near the middle of the shaft. The bony fibers in the scapula of *Trionyx*, as shown in figure 2, do not depart from this plan of formation.

The fibers are not found to be densest near the center of the

shaft of each prong, but at the base of the V, where we would expect it if the scapula were a single element. The threads of bony matter are seen running in both directions and along the sides of each prong from the base of the V where they have their origin. At the base of the V the fibers are most compact, and here is the center of ossification for the scapula. In order to be sure that the single condition was found in early embryonic life before ossification sets in, sections have been made which show that there is no separation in the early stages of the element, and that both prongs originate synchronously. The fibers do not occur in the glenoid fossa but are present on the inner side of the V. The glenoid cavity, as stated by Rathke, remains cartilaginous.

Rathke has obtained practically the same result in some forms, and in others he secured results which would seem to be contradictory. His final conclusion is that there are two elements in the scapula, although he studied forms which showed clearly but one ossific center. Hulke[8] has rather misinterpreted Rathke and converts the embryologist's language into meaning that he had discovered two centers of ossification for this bone. As a matter of fact, the fibers of bone when laid down are very difficult to see in the early stages. Especially would this be true in dissected specimens, and it is no wonder that Rathke thought there were two in some and one in others. That he did discover forms in which there was but a single center is evident from the following: "In jedem Stücke aber geschiet dies[9] nicht, . . . an zwei Stellen, sondern nur an einer, und zwar in der Nähe der Grube für das Schultergelenk . . ." Parker, working some sixteen years later, came to the latter conclusion in regard to the scapula, for he says, four years after his investigations: "This front fork forms with the scapula a gentle arc; it is of the same thickness, nearly the same length and has no separate osseous center, the two bars being hardened by one ectosteal sheath."[10] Baur has called the anterior ray of the scapula the "proscapula," but Andrews suggests that a better term would be the proscapular process, since the former term implies the existence of a separate element.

There is no great similarity in the fundamental structure

8. Hulke, 1893, Proc. Roy. Soc. Lond., p. 249.

9. Rathke, 1848, Ent. Schild., p. 139.

10. Parker, 1868, Structure of Shoulder Girdle, Ray Society, p. 141.

of the scapula of turtles and plesiosaurs. In the turtles the element is fundamentally biradiate, but in the plesiosaurs it is merely a curved plate-like element, which hardly has the appearance of the V, so characteristic of the Chelonia. The radiate character of the scapula of plesiosaurs is ontogenetic, as Andrews has shown.[11] The scapula of turtles early assumes the V shape, and this is evident in very young embryos. The radiate character of the plesiosaurian scapula is not attained until the animal becomes adult. The three rays thus formed by the growth of the outer process was used by Hulke for correlation with the shoulder girdle of the turtles. But this correlation falls to the ground when we learn that the third ray of the chelonian girdle corresponds morphologically with the broad pectoral element, the coracoid, of the plesiosaurs. It has been shown above that the turtle scapula is a single element, and the singleness of the plesiosaurian scapula is vouched for by Seeley, Baur and Williston. "As to the structure of the scapula, all students of the plesiosaurs are now agreed that the procoracoid does not unite with the scapula, . . ."[12] The scapulæ of turtles and plesiosaurs are analogous in their form but they differ greatly and fundamentally in the two groups by the formation of the third ray in plesiosaurs. Seeley[13] has agreed with the results above given. He likewise was of the opinion that Hulke had misinterpreted Rathke. Hulke's greatest error lay in giving a portion only of Rathke's results and taking that portion as positive evidence for two ossific centers. Seeley objects strongly to the idea that there is any procoracoid in the scapula of the plesiosaurs and disclaims any relationship between turtles and plesiosaurs on the basis of the structure of the shoulder girdle.

The whole discussion of the relationship of turtles and plesiosaurs, as based on the elements of the pectoral girdle and the "epiphyses," has revolved around structures which are not present in either group. Neither group has epiphyses, and in neither group is the scapula composite. There is thus no basis for an affinity on the ground of these structures.

The claim that the broad pectoral and pelvic elements of the plesiosaurs are homologous to the plastron of turtles can hardly be valid. The broad character of the girdles in the

11. Andrews, 1895, Ann. and Mag. Nat. Hist., ser. 6, vol. XV.

12. Williston, 1907, Proc. U. S. Nat. Mus., vol. 32, p. 488.

13. Seeley, 1893, Proc. Roy. Soc. Lond., p. 161.

plesiosaurs is a secondary character, and whatever resemblance there may be is merely a parallel one. The coracoid of the plesiosaurs, which forms the broadest element in the girdle, finds its homologue in the coracoid of the turtles which is *within* the plastron and forms no part of it. The same may be said of all of the elements of the pelvic girdle. The elements which are supposed to form the plastron are the ventral ribs, the interclavicle and clavicles. All of these structures are present in the plesiosaurs, but they are also found in the ichthyosaurs and nothosaurs.

Williston has recently shown[14] that there can be no grounds for relationship between the two groups on the structure of the skull, and disclaims any relationship on the structure of the vertebræ and paddles. The skull of the turtle is as far removed in its structure from that of a plesiosaur as it well can be. In the turtles the skull is completely roofed over, and there is not a vestige of a temporal bar or vacuity. It is known as the stegocrotaphous type of cranium. The plesiosaurs, on the other hand, have the mammalian type of cranium, and possess but a single bar and a single enclosed vacuity. This type of skull Williston calls the therocrotaphous. It would be incongruous to relate two groups of animals in which the crania are of such widely varying types as are the skulls of the turtles and plesiosaurs.

There is a similarity in the mode of life of the two groups, since both are largely of littoral habits. The similarity of "form and habits of these two orders of animals has been due solely to parallel evolution, to similar aquatic conditions." (Williston.) There is decidedly more similarity in the form and mode of life of the ancient ichthyosaurs and the modern dolphins, but no one has ever seriously considered relating these two groups.

The relationship between the turtles and plesiosaurs has therefore been based, in large part, on misconceptions, and the animals do not have the structures on which the greater claims for affinity have rested. "The plesiosaurs could not have been derived from any ancestors that might by the widest stretch of the imagination be called Chelonia or Chelonia-like. Nor could the turtles have come from any forbears even suggesting the sauropterygian structure" (Williston).

14. Williston, 1907, Proc. U. S. Nat. Mus., vol. 32, p. 488.

SUMMARY.

1. The grounds on which have been based the relationship between the turtles and plesiosaurs are (1) the elongate character of the neck and tail claimed for certain turtle embryos; (2) the presence of epiphyses on the long bones; (3) the fusion of the procoracoid to the scapula in the two groups; (4) the possession of teeth in the two groups; (5) the girdles of the plesiosaurs have been compared to the plastron of the turtles; and (6) the similarity in form and habits of life.

2. There are but eight segments in the neck of the turtle embryos examined. There are from thirteen to seventy-six cervical vertebræ in the plesiosaurs, according to Williston.

3. There are no epiphyses on the long bones of either turtles or plesiosaurs. The structures called "epiphyses" are the endochondral cones found in all groups of the Sauropsida.

4. The scapula of the turtle is a single element and the procoracoid is not present. The method of formation of the element is greatly different in the two groups.

5. The elements of the pectoral and pelvic girdles in the plesiosaurs are not homologous with the plastron of the turtles.

6. The structure of the skull and the entire organization of the animals is proof against relationship between the two orders.

7. The similarity of form and habits of life are due to parallel evolution and adaptation for existence under similar conditions.

I am indebted to Dr. S. W. Williston for many valuable suggestions and for several references. It was at his instance that the study was first undertaken.